

## HOST-SPECIFICITY AND CORRESPONDING EVOLUTION IN MONOGENEAN FLATWORMS AND VERTEBRATES

BY

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Host-specificity, i.e. the restriction of particular species of parasites to their respective specific hosts is of almost universal occurrence in monogeneans (Bychowsky, 1957; Llewellyn, 1957) but there are some exceptions, e.g. *Benedenia melleni* on numerous species of marine fishes and *Diplozoon paradoxum* on several species of freshwater fishes. In addition there are some cases where a parasite species is restricted to several species of a particular host genus, e.g. *Calicotyle kroyeri* on species of *Raja*, or to different genera of a particular family, e.g. *Plectanocotyle gurnardi* on various genera of Triglidae. However, it is possible that further investigations might reveal that in *Plectanocotyle* there are in fact different species of parasites. Thus it may be concluded that restriction to particular hosts is of general occurrence in monogeneans and that it is most commonly expressed as a species-specific relationship.

Two kinds of specificity may be recognized and both may be illustrated by entodellid monogeneans: (a) phylogenetic specificity ("conjugate evolution", "phylogenetic parallelism") when related parasites occur on related hosts, e.g. *Entodella soleae* and *E. hippoglossi* on their respective heterosomatid teleosts *Solea solea* and *Hippoglossus hippoglossus* and (b) ecological specificity when related parasites occur on unrelated hosts sharing a common habitat, e.g. *E. soleae* and *E. hippoglossi* on flat bottom-dwelling teleosts, and *E. diadema* on the flat bottom-dwelling elasmobranch *Dasyatis pastinaca*. The occurrence of further entodellids e.g. *E. corona* on another dasyatid *D. americana*, could mean that there have been two parallel ecological crossovers, but a more probable explanation is that following a single initial ecological transfer there was subsequent corresponding speciation between parasites and hosts.

The occurrence of strict species-specificity, with "closely" related parasites being restricted to similarly related hosts, can be explained only as a result of corresponding speciation of parasites and hosts: as a host stock diverged, monogeneans on the "daughter" species could have survived only by becoming adapted to any "new" features of the new host, whether they were structural, physiological, or behavioural. It is very probable that speciation among hosts has sometimes presented insurmountable hazards for the parasite, as may be inferred from the occurrence of dichidophorans on gadids (Llewellyn & Tully, 1969). Presumably an ancestral gadid harboured a host-specific *Dichidophora* species, and as the host stock diverged to give rise to *Micromesistius*, *Pollachius*, *Merlangius* (*Odontogadus*), etc., so the parasite stock kept pace in diverging correspondingly into *Dichidophora minor*, *D. denticulata* (and *D. pollachius*) and *D. merlangi* respectively. The process is still going on, and *D. esmarkii* appears not yet to be restricted to either *Trisopterus esmarkii* or *T. minutus* but, in areas where the host distributions overlap, to be able to parasitize both these gadids (Llewellyn, Macdonald and Green, 1980). However, many, and perhaps most, gadids appear to have lost their dichidophoran parasites (Llewellyn and Tully, 1969), and in European waters the cod *Gadus morrhua* and the haddock *Melanogrammus aeglefinus* are examples of gadids known not to harbour a dichidophoran.

If now the above situation with respect to corresponding speciation in gadids and dichidophorans is assumed to be typical of the general picture of corresponding evolution in vertebrates and their

monogenean parasites, it follows that it is extremely likely that many monogenean stocks will have flourished and subsequently become extinct. Indeed, since it has been estimated that most (> 90 % ?) of the palaeozoic animal species became extinct at the end of that period, the inference is that modern monogeneans differ substantially, in both numbers and variety of species, from their palaeozoic ancestors. In the absence of fossil monogeneans, it may be pertinent to consider further parallelism with other animals: there is considerable evidence for evolutionary stasis, e.g. some vertebrates are thought not to have changed much since palaeozoic times. Then, since many monogenean infections are uni-specific with "congeneric pairs" being relatively rare, and with the evolution of monogeneans being more a matter of "competition with the host" than of intra-specific competition, it is to be expected that some present-day monogeneans may well be relicts.

### THE NATURE OF SPECIFICITY

The physiological basis for host-specificity was for a long time surmised (e.g. by Nyhelin and by Bychowsky) to be "haemotactic", but experimental evidence supporting the hypothesis awaited the elegant investigations of Kearn (1967) on host-finding in *Entobdella soleae* which showed that the attachment of the oncomiracidium took place only after recognition of the specific mucus of the host. Such chemo-reception does not, however, appear to be universal among monogeneans since Paling (1969) found that larvae of *Disocotyle sagittata* did not respond to mucus from its host *Salmo trutta*. But whatever the mechanics of host-recognition may be, successful establishment appears to be restricted to a particular host or hosts.

Under experimental conditions Izjumova (1970) and Molnar (1971) found that some larval dactylogyrids, even if they very occasionally became attached to unusual species of hosts, persisted only a short time and disappeared before reaching sexual maturity.

In the course of various investigations of several parasite-host systems, e.g. *Gastrocotyle trachuri* and *Pseudaxine trachuri* on *Trachurus trachurus* and *Plectanocotyle gurnardi* on *Trigla cuculus*, thousands of parasites (including early larvae) have been recorded from thousands of hosts by my students and me, but in only one parasite-host complex (*Dididophora* spp./*Trisopterus* spp, see p. 289) has a parasite other than the expected one been observed, and this unusual occurrence has been interpreted as "evolution in action" (see Llewellyn, Macdonald and Green, 1980).

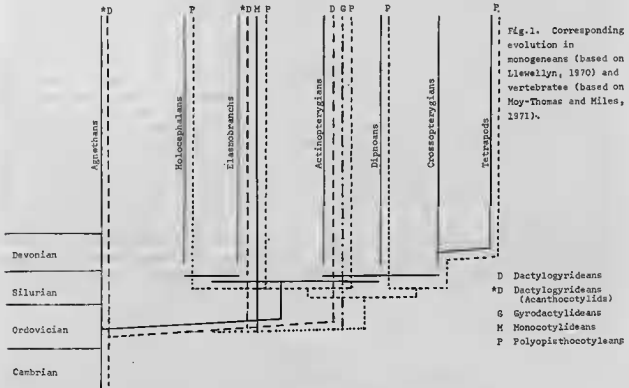
Ktari (1971) found gastrocotylid and hexostomatid post-larvae, but no adults, on unusual hosts; moreover such larvae had usually reached the same stage of what was thought to be arrested development. While bearing in mind the possibility that such post-larvae were utilizing intermediate hosts, as had been postulated by Bychowsky and Nagibina (1967), Ktari nevertheless was of the opinion that the post-larvae were unable to continue development on their unusual hosts and were doomed to perish.

It may be concluded then that "selection" of the specific host is obligatory for the successful establishment of the parasite; other factors, e.g. size compatibility, appropriate attachment apparatus, etc., may be important for the subsequent maintenance of the specific relationship, but the primary factor is some physiological phenomenon acting at the time of invasion. If such a factor, e.g. a chemical attractant in the skin-mucus of the normal host were by chance present in the mucus of an unrelated fish in the same habitat, an opportunity for ecological transfer might occur.

### CORRESPONDING EVOLUTION IN MONOGENEANS AND THEIR HOSTS

The relationship between the major groups of monogeneans and their hosts is illustrated in Fig. 1 in which the phylogeny of the hosts is based on Moy-Thomas and Miles (1971) and that of the

parasites on Llewellyn (1970). The scheme for monogeneans is based mainly on studies of ontogeny which have revealed patterns of consecutively developing primary (marginal hooks), secondary (hamuli) and tertiary (baptoral loculi, clamps/suckers, pseudohaptoral plectana, etc.) attachment organs accompanied by corresponding variations in the feeding apparatus and some other features (Llewellyn, 1970). This scheme differs substantially from Bychowsky's (1957) classification based mainly on the numbers of marginal hooks in the larva (see Llewellyn, 1970) but recognizes the same four (or five) major groups as Lambert's (1980) phylogenetic scheme based mainly on patterns of ciliated epidermal cells and of sensilla in the larva.



The present evolutionary scheme has been amplified by the inclusion of information I have been privileged to receive, before its publication, from Dr. G. Malmberg of Stockholm and Mr. T. McDonald of Nanaimo, about acanthocotylids which they, quite independently of each other, have discovered on myxiniids. The phylogenetic significance of these new host records is the inference that acanthocotylids appear now to be the most "ancient" of living monogenean parasites. However, their possession of a pseudohaptor and of a pair of centrally-placed marginal hooks on the larval haptor indicates that, though occurring on the "oldest" of vertebrates (Agnathans), they are likely to have diverged already from the protomonogenean (assumed to have all its marginal hooks on the periphery of the haptor, to have hamuli between marginals II and III and to lack a pseudohaptor).

A further consequence of the discovery of acanthocotylids on agnathans is the inference that dactylogyrideans had already differentiated in Ordovician times, and when this is considered alongside the radiation of the polyopisthocotyleans with their gnathostome hosts in the Devonian, it follows that the two largest groups of modern monogeneans were already distinct in Palaeozoic times. Moreover, there is no evidence to suppose that the other two major groups, the monocotylideans and gyrodactylideans, did not arise at about the same time. If then all these four main groups of monogeneans had already differentiated in the palaeozoic, and may indeed have shared a common host-stock, relicts of them may have persisted on any of the vertebrate lines which arose at that time. This

might explain the enigmatic occurrence of some monogeneans on "unusual" hosts e.g. *Euzetrema* as a dactylogyridean on an urodele, *Amphibdelloides* as a dactylogyridean on the elasmobranch *Torpedo*, and *Enoplocotyle* as a protoacanthocotylid dactylogyridean on the teleost *Muraena*. It remains very probable however, that some curious host-parasite associations e.g. *Oculotrema* on *Hippopotamus* and *Isancistrum* on the cephalopod *Alloteuthis* are the results of ecological transfer. Against the above background it is possible to speculate that the earliest monogeneans may have diversified while sharing a common host stock, the earliest vertebrates. Later, the main groups of parasites became increasingly committed to various diverging host stocks, remaining evolutionarily "static" until the "explosions" of dactylogyrideans, gyroductylideans and mazoeraoidean polyopisthocotyleans on the teleosts. If then the major divergences in monogeneans took place in the Palaeozoic, the evolutionary time scale would be very different from that of Bychowsky (1957, Fig. 310) where the main groups are represented as having arisen in the Mesozoic, i.e. long after the separation of the major groups of hosts.

If there has in fact been a general correspondence in the evolution of monogeneans and vertebrates, then it is possible that interpretations of evolutionary pathways in the parasites could help in solving problems of vertebrate phylogeny. Since the interrelations of the various major groups of vertebrates are unknown, all of them appearing to have been distinct when first present in the fossil record (Nelson, 1976), they have been linked to each other by various palaeontologists in almost as many ways as the mathematical combinations permit. The present brief review of corresponding evolution suggests that, on the evidence of the inter-relationships of polyopisthocotyleans, where the polystomatid parasites of dipnoans and tetrapods, with their unarmed haptor suckers, appear to be nearest the original stock, an ancestral dipnoan/tetrapod (perhaps the crossopterygians lost their polystomatids) may have been the most primitive group of gnathostomes, a view for which there would be some support from palaeontology (e.g. Jarvick, 1968). If, however, the weight of evidence about vertebrate ancestry should show convincingly that dipnoans and tetrapods arose later than elasmobranchs and actinopterygians, which are the hosts of polyopisthocotyleans with armed suckers, then there would be an increased need for parasitologists to attempt to determine whether the polystomatid suckers are secondarily simple through having lost their sclerites.

## REFERENCES

- BYCHOWSKY, B. E., 1957. — *Monogenetic trematodes, their classification and phylogeny*. Moscow : Leningrad Academy of Sciences, USSR.
- BYCHOWSKY, B. E. and NAGAIINA, L. F., 1967. — On « intermediate » hosts of monogeneids (Monogenoidea) Akademi Nauk SSR, *Parasitology* (USSR), 1, 117-24.
- FZJUMOVA, N., 1970. — On the specificity of some species of the genus *Dactylogyrus* Diesing 1850. *Parasitology* (USSR), 4, 466-72.
- JARVICK, E., 1968. — Aspects of vertebrate phylogeny. *Nobel Symposium*, 4, 497-527.
- KEARN, G. C., 1967. — Experiments on host-finding and host-specificity in the monogenean skin parasite *Entobdella soleae*. *Parasitology*, 57, 585-605.
- KTARI, M. H., 1971. — Recherches sur la reproduction et le développement de quelques monogènes (Polyopisthocotyles) parasites de poissons marins. Thesis : Université de Montpellier.
- LAMBERT, A., 1980. — Oncomiracidiums et phylogénèse des Monogenea (Plathelminthes). *Annales de Parasitologie* (Paris), 55, 281-325.
- LLEWELLYN, J., 1957. — Host-specificity in monogenetic trematodes. In *First symposium on host specificity among parasites of vertebrates*, Neuchâtel : Paul Attinger.
- LLEWELLYN, J., 1970. — Taxonomy, genetics and evolution of parasites. Monogenea. Proceedings of Second International Congress of Zoology. *Journal of Parasitology*, 56 (4, Section 2, Part 3), 493-504.
- LLEWELLYN, J., MACDONALD, S., and GREEN, J. E., 1980. — Host-specificity and speciation in dielidophoran

(monogenean) gill parasites of trisopteran (gadoid) fishes at Plymouth. *Journal of the Marine Biological Association, U.K.*, 60, 73-9.

- LLEWELLYN, J. and TULLY, C. M., 1969. — A comparison of speciation in didelphophorean monogenean parasites and in their fish hosts. *Journal of Fisheries Research Board of Canada*, 26, 1063-74.
- MOLNAR, K., 1971. — Studies on gill parasitosis of the grass carp (*Ctenopharyngodon idella*) caused by *Dactylogyrus lamellatus* Achmerov, 1952. *Acta Veterinaria Academiae Scientiarum Hungaricae*, 21, 267-89.
- MOY-THOMAS, J. A. and MILES, R. S., 1971. — *Palaeozoic Fishes*. London : Chapman and Hall.
- NELSON, J. S., 1976. — *Fishes of the world*. New York, London : John Wiley and Sons.
- PALING, J. E., 1969. — The manner of infection of trout gills by the monogenean parasite *Discocotyle sagittata*. *Journal of Zoology London*, 159, 293-309.

## DISCUSSION

BURT. — Which forms have tanned eggs ?

LLEWELLYN. — All except *Gyrodactylus*. This would serve to allow passage of eggs through the gut of crustacean, etc... Tanned eggs also occur in Turbellarians.

LAMBERT. — Does the specificity operate at the level of host infestation, for example fixation onto the host surface ?

LLEWELLYN. — Possibly, but we have only one example of the oncomiracidium of a species being capable of identifying host mucus.

BURT. — One of my students has shown the same phenomenon for an ancyrocephaline on perch.

BOURGAT. — Le modèle de l'angle de l'exigence de fixation s'applique parfaitement aux oncomiracidiums de *Polystoma* qui sont, expérimentalement, capables de se fixer sur plusieurs espèces de têtards d'Amphibiens. L'angle d'exigence de fixation est donc large.

Il est limité, dans un premier temps, par les conditions éco-éthologiques : dans la nature, un oncomiracidium ne rencontre pas n'importe quel têtard, comme cela lui est donné en laboratoire.

L'angle d'exigence de développement est, lui, très limité, et, pratiquement, une seule espèce de *Polystoma* parvient à se maintenir sur une espèce d'Amphibien et à franchir le cap des métamorphoses de l'hôte.

DUPOUY. — A partir de quel groupe de poissons s'est opérée la divergence entre les Monopisthocotylea et les Polyopisthocotylea ?

LLEWELLYN. — We cannot give a precise answer, probably before the Devonian.